Shell Form and Burrowing Performance in Gastropods from Pacific Panama, with Comments on Regional Differences in Functional Specialization

by

ELIZABETH C. DUDLEY

Department of Zoology, University of Maryland, College Park, Maryland 20742, USA

AND

GEERAT J. VERMEIJ

Department of Geology, University of California, Davis, California 95616, USA

Abstract. A study of the burrowing performance of 22 species of gastropods from Pacific Panama revealed that a smooth external shell surface and a large foot were associated with rapid burrowing, whereas a sculptured surface and a small foot (associated with a tall spire or a slender body whorl) characterized slow burrowers. Comparison with an earlier study of 33 gastropod species from Guam suggests that Indo-West Pacific species are more specialized in the development of shell characters related to both antipredatory resistance and burrowing despite the general incompatibility between these two directions of functional specialization.

INTRODUCTION

Infaunal burrowing gastropods have been a conspicuous element of communities on shallow-water tropical sandy and muddy bottoms since Late Mesozoic time (VERMEIJ, 1987). In order to trace the history and evolution of the burrowing habit in gastropods, it is desirable to establish a functional relationship between shell architecture and burrowing performance in living species. In a previous study (VERMEIJ & ZIPSER, 1986), based on 33 burrowing gastropod species from the island of Guam in the tropical Indo-West Pacific region, rapid burrowing was found to be associated with a large foot (and usually a large shell aperture or the ability to extend the foot over the shell) and with a smooth external shell surface. Slow burrowers tended to have a small aperture (associated either with a high spire or with a slender body whorl) and well-developed shell sculpture (especially spiral cords). Ratchet sculpture, in which the anterior slopes of spiral elements are less steep than the posterior slopes, enhance burrowing performance in some high-spired species (SIGNOR, 1983),

but it is found typically in relatively slow burrowers. Among species with a slender body whorl, those of a wedge-shaped conical aspect may have a small advantage over more cylindrical types, but again species of this shape are usually slow. Most gastropods in Guam were found to be sluggish burrowers.

The present study was undertaken to determine if similar functional relationships apply to a taxonomically quite different assemblage of burrowing gastropods in the rich biota of Pacific Panama. A secondary objective was to ascertain if the assemblages from Guam and Panama differ with respect to the burrowing performances of their component species. There is reason to expect such a difference. Previous studies have suggested that antipredatory resistance (great retractability of the soft parts, a narrow or toothed aperture) is better developed in Indo-West Pacific than in tropical American infaunal gastropod assemblages (VERMEIJ, 1978; VERMEIJ et al., 1980). Given that such resistance is usually associated with a small aperture and therefore with slow burrowing, it might be expected that

Table 1

Burrowing performances of Panamanian gastropods.

Species	N_i	N_t	BRI	AS	SH	Sculpture
Natica grayi Philippi, 1850	2	4	0.60 ± 0.20	—	1.09	smooth
N. unifasciata Lamarck, 1822	8	15	0.71 ± 0.26	—	1.17	smooth
Polinices uber (Valenciennes, 1832)						
Burrowing with cyclical movement	4	8	0.75 ± 0.20	—	1.23	smooth
Burrowing without cycles	2	4	2.20 ± 0.40			
P. panamensis (Recluz, 1844)	2	3	0.91 ± 0.06	—	1.07	smooth
Phalium centiquadratum (Val., 1832) juvenile	1	2	0.61	1.40	1.27	ratchet
Strombina bicanalifera (Sowerby, 1832)	4	4	0	1.71	1.48	smooth
Northia pristis (Deshayes in Lamarck, 1844)	1	2	0.69	1.52	1.95	smooth
Cymatophos fusoides (C. B. Adams, 1852)	1	2	0.16	1.47	1.93	axial
Nassarius complanatus (Powys, 1835)	1	2	1.23	1.32	1.33	cancellate
N. luteostomus Broderip & Sowerby, 1829	5	10	0.41 ± 0.19	1.30	1.35	nodose
N. scabriusculus (Powys, 1835)	1	2	0.06	1.27	1.79	axial
Olivella semistriata (Gray, 1839)	7	13	0.57 ± 0.11	—	1.39	smooth
O. volutella (Lamarck, 1811)	4	7	0.72 ± 0.46	—	1.51	smooth
Agaronia testacea (Lamarck, 1811)	3	6	1.66 ± 0.93	—	1.24	smooth
Cancellaria mitraeformis Sowerby, 1832	2	4	0	2.85	1.50	cancellate
Conus mahogani Reeve, 1843	4	7	0.18 ± 0.05	10.7	1.24	smooth
Pilsbryspira aterrima (Sowerby, 1834)	1	2	0.21	3.32	1.84	axial
Terebra glauca Hinds, 1844	3	6	0.25 ± 0.06	1.38	2.99	cancellate
T. hancocki Bratcher & Burch, 1970	1	2	0	1.67	3.62	cancellate
T. puncturosa Berry, 1958	1	2	0	1.19	4.13	axial
T. robusta Hinds, 1844	1	2	0	1.64	3.95	axial
T. strigata Sowerby, 1825	1	2	0	1.45	2.95	axial

Key: N_i—Number of individuals. N_t—Number of trials. AS—Aperture shape: aperture length divided by aperture width. SH—Spire height: shell height divided by aperture height. BRI—Burrowing rate index: cube root of wet weight divided by time in seconds for complete burial.

MATERIALS and METHODS

In February of 1986, we collected 22 gastropod species from Playa Venado and two beaches near the Smithsonian Tropical Research Institute's marine laboratory at Isla Naos, on the Pacific coast of Panama. Individual animals were held at the laboratory for one to two days in tanks with a bottom layer of sand and running seawater. We conducted the burrowing trials in a small aquarium containing seawater and a 5-cm layer of coarse sand (6% gravel-pebble fraction, 19% very coarse sand, 34% coarse sand, 27% medium sand, 8% fine sand, 4% very fine sand, and 3% silt by weight). This sand was roughly similar to that used in the trials at Guam, in which the coarse-sand and medium-sized-sand fractions were 56% and 46% by weight respectively (VERMEIJ & ZIPSER, 1986). The sand was covered with a thin film of water. For each trial, we placed an individual snail on the sand surface, and recorded burrowing time in seconds, starting with the first burrowing movements that the animal made with its extended foot. The trial was ended when the animal was completely buried or when no additional burrowing movements occurred for a period of at least one minute. Once the animal was either completely buried or had ceased moving, we extracted it, redistributed the sand in the aquarium, and

placed the animal on the surface of the sand for a second trial. At the end of the second trial, we dried the animal's shell surface with a paper towel, took the wet weight of the animal in grams, and measured apertural and overall shell dimensions in millimeters. The wet weight inevitably included some water in the shell. We could have measured volume instead of weight in order to alleviate this potential source of error, but it would have introduced other errors; moreover, our previous work in Guam was also based on wet weight. We did not measure the apertural dimensions of olivids and naticids, because these snails extend the foot over the exterior surface of the shell; as a consequence, the limits of the aperture are ill-defined, and in any case do not correspond with foot size.

We evaluated burrowing performance by calculating the burrowing-rate index (BRI), defined by STANLEY (1970) as the cube root of animal mass (wet weight) in grams divided by burial time in minutes. This size-independent quantity makes possible comparisons among species varying in size, architecture, and provenance (see STANLEY, 1970, and VERMEIJ & ZIPSER, 1986, for further discussion and documentation).

RESULTS and DISCUSSION

The relationship between shell form and burrowing performance observed in gastropods from Guam was also evident in the Panamanian fauna (Table 1). The 10 species
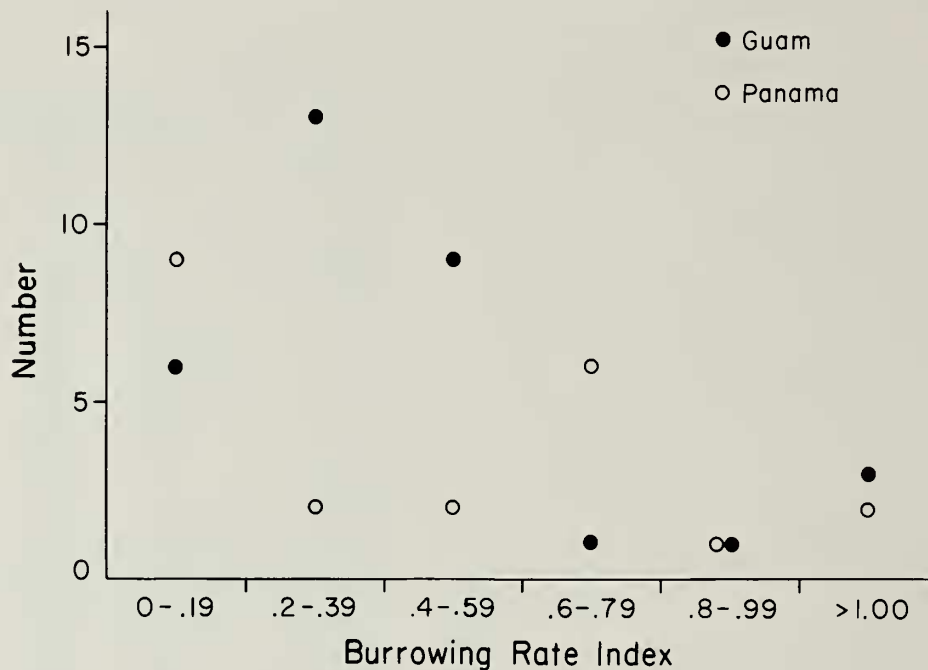
Figure 1

Comparison of burrowing rate indices of gastropods from Guam (closed circles) and Panama (open circles). Each circle represents the number of species in the indicated interval.

with smooth body whorls had significantly higher burrow-ing-rate indices (BRIs) than did the 12 sculptured species (P < 0.05, Mann-Whitney U-test). Only one of the 10 smooth-shelled species (*Strombina bicanalifera,* 10%) did not burrow completely during laboratory trials, as com-pared with five of 12 sculptured species (42%). Among the sculptured species, the one with ratchet sculpture (juvenile *Phalium centiquadratum*) ranked second highest in bur-rowing performance. If the 10 species represented by only a single individual are removed from the analysis, the difference in burrowing performance between the eight smooth and four sculptured species still holds (P < 0.05). The BRIs of the sculptured species all fall below the overall median of 0.49, whereas six of the eight smooth-shelled species fall above the median.

Small apertures were associated with slow burrowing. The three species with a narrow aperture (aperture length-width ratio 2.50 or higher) and without the ability to extend the foot over the shell were all poor burrowers; one (*Cancellaria mitraeformis*) did not burrow completely, and the other two (*Conus mahogani* and *Pilsbryspira aterrima*) had BRIs of only 0.18 and 0.21 respectively. The five high-spired species (all terebrids) had very poor burrowing abilities; four of the five failed to burrow completely, and the fifth (*Terebra glauca,* the only species with more than one representative) had a mean BRI of only 0.25, a value well below the median of 0.33 for the assemblage of 22 species.

Species that prey on mollusks or echinoderms were by

far the fastest burrowers relative to their mass. These species, which belong to the families Naticidae, Cassidae, and Olividae, have a large foot, which is used both for burrowing and for capturing and suffocating prey (MARCUS & MARCUS, 1959; HUGHES & HUGHES, 1981; HUGHES, 1985).

The spectrum of burrowing performances was similar in the Panamanian and Guamanian assemblages (Figure 1). The median BRI was 0.33 in both assemblages, and the number of fast burrowers (BRI 1.0 or higher) consti-tuted 9% of the assemblages in both regions. Slow bur-rowers (BRI 0.25 or less) are slightly (but not significantly) better represented in Panama (11 of 22 species, 50%) than in Guam (10 of 33 species, 30%). If all species represented by only a single individual are removed from the analysis, the median BRIs in Panama and Guam are 0.49 (n = 12) and 0.37 (n = 22) respectively; rapid burrowers con-stitute 8% and 9% of the assemblages, and slow burrowers make up 42% and 32% of the assemblages from Panama and Guam respectively.

Despite the overall similarities, comparisons within families suggest that Panamanian species are somewhat poorer burrowers than are species from Guam. The three olivids from Panama all had lower BRIs than the two species from Guam. The five Terebridae from Panama had significantly lower BRIs than the six species from Guam. Only one of the five conids from Guam ranked below the Panamanian *Conus mahogani* in relative bur-rowing performance. The families Columbellidae and

Table 2

Incidence of traits related to burrowing performance in assemblages from Panama and Guam.

	Panama		Guam	
	Number of		Number of	
Trait	species	Percent	species	Percent
Smooth surface	10	45	14	42
Ratchet sculpture	1	4.5	4	12
Conical outline	1	4.5	7	21
Large aperture or foot	10	45	4	12
Narrow aperture or tall spire	8	36	31	94

Turridae were each represented in the two assemblages by one species; in both cases, the species from Panama had a lower BRI than did the species in Guam. No consistent difference in burrowing performance was, however, evident in the Naticidae and Nassariidae.

Although these comparisons are based on perilously small numbers of species and individuals, they suggest a difference in burrowing performance opposite to the one expected on the basis of the expression of traits related to antipredatory resistance in the two faunas. Even if further work should show that the within-family differences in burrowing performance between Guam and Panama are insignificant, the expected pattern that species in Guam should on average be poorer burrowers than those in Panama because of the greater development of antipredatory resistance is not borne out. Of the 33 species whose burrowing performance was evaluated in Guam, 31 (94%) showed clear specializations for morphological resistance to shell-breaking predators (that is, a tall spire, associated with deep retractability of the soft parts, and a narrow aperture). The corresponding number among the 22 Panamanian species was only eight (36%). These values (Table 2) are representative of the sand-dwelling molluscan biotas of the Indo-West Pacific and eastern Pacific respectively. The species from Guam have, to some extent, overcome the basic incompatibility between effective burrowing and effective armor. This is suggested by the higher incidence of several burrowing specializations there than in Panama (Table 2). This greater specialization is evident even within families. Many shallow-water Terebridae in the Indo-West Pacific region are smooth-shelled, whereas in the eastern Pacific such species constitute a small minority (VERMEIJ et al., 1980). The same is true in the Nassariidae and Mitridae. Cone-shaped burrowers, in which a wedge-shaped leading edge is effectively combined with a narrow

aperture, are found only among Conidae and the harpid genus *Morum* in the eastern Pacific, whereas in the Indo-West Pacific they occur in these groups as well as in the Mitridae, Turridae, and Strombidae. Ratchet sculpture is rare in tropical American gastropods. In the one species with this sculpture that we examined in the present study (*Phalium centiquadratum*), the ratchet effect occurs only in juvenile shells. In Indo-West Pacific faunas, ratchet sculpture is found in several species of *Rhinoclavis* (Cerithiidae), *Neocancilla* (Mitridae), *Terebra* (Terebridae), and *Pupa* (Actaeonidae), among others.

Despite the very limited scope of the present study, we believe that comparative studies of functional performance of species from different parts of the world are potentially informative. They may reveal unsuspected differences that in turn prompt further questions about the evolutionary conditions and events that have shaped modern faunas.

ACKNOWLEDGMENTS

LITERATURE CITED

HUGHES, R. N. 1985. Predatory behaviour of *Natica unifasciata* feeding intertidally on gastropods. Jour. Moll. Stud. 51:331–335.

HUGHES, R. N. & H. P. I. HUGHES. 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). Malacologia 20:385–402.

MARCUS, E. & E. MARCUS. 1959. Studies on "Olividae." Boletim da Faculdade de Filosofia, Ciencias e Letras, São Paulo 232(Zoologia, 22):99–188.

SIGNOR, P. W., III. 1983. Burrowing and the functional significance of ratchet sculpture in turritelliform gastropods. Malacologia 23:313–320.

STANLEY, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geol. Soc. Amer. Memoir 125:1–296.

VERMEIJ, G. J. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press: Cambridge. 332 pp.

VERMEIJ, G. J. 1987. Evolution and escalation: an ecological history of life. Princeton University Press: Princeton. 527 pp.

VERMEIJ, G. J. & E. ZIPSER. 1986. Burrowing performance of some tropical Pacific gastropods. Veliger 29:200–206.

VERMEIJ, G. J., E. ZIPSER & E. C. DUDLEY. 1980. Predation in time and space: peeling and drilling in terebrid gastropods. Paleobiology 6:352–364.